Chapter 9

Free Radicals and Antioxidant System in Seed Biology

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Additional information is available at the end of the chapter

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Abstract

Reactive oxygen species (ROS) are involved in various development stages of seed biology. During seed desiccation, germination and aging, oxidative stress may increase in higher levels, leading to cellular damage and seed deterioration. Plant cells have antioxidant system, detoxifying enzymes and antioxidant compounds, that scavenge ROS, participating in seed survival. This antioxidant system has various roles in desiccation and germination of developing seeds, seed storability, and seed aging. On the other hand, ROS are accepted as molecules involving in cellular signaling, and having regulatory functions in seed development. ROS are also found to have roles in gene expression in early embryogenesis, dormancy and germination. Abscisic acid is a plant hormone and a signaling molecule in seed development and that is reported to have relationships with ROS. The objective of this article is to review the roles of ROS and the importance of antioxidant system in orthodox seeds, and to emphasize the dual effects of ROS in seed biology.

Keywords: free radicals, reactive oxygen species (ROS), antioxidant, seed biology, ROS signaling

1. Introduction

ROS are usually thought as hazardous molecules, attacking to biomolecules, leading to membrane and DNA injuries, and deleterious effects in seed germination processes [1–5]. Seed aging is a process that the roles of ROS are well documented [6–9]. ROS also have damages in desiccation of seeds by dehydration [10, 11]. Although ROS have been considered as detrimental to seeds up to now [12–16], recent advances in plant physiology signaling pathways have led to reconsider their role [17–29]. ROS accumulation can therefore be also beneficial for seed germination and seedling growth by regulating cellular growth, providing a protection against pathogens, and controlling the cellular redox status [30–33]. ROS are

also proved to act as a positive signal in seed dormancy release [30–33]. The dual function of ROS in plants depends on the levels of antioxidant compounds, and enzyme activities release [34–38]. By this way, plants can eliminate potentially harmful ROS that is produced under stress conditions, or control ROS concentrations in order to regulate various signaling pathways [34–38]. This dual function of ROS is a very interesting subject in seed physiology. Even though there is a huge progress in this field, and the dual functions of ROS are quite well documented in the literature, it should also be regarded from a different point of view. The involvement of ROS in seed filling processes is not well documented, and the mobility of ROS in seeds has not yet been documented, thus, more data is needed on roles of ROS in seed germination and development physiology. Under light of the increasing progress made in the understanding of mechanisms driven by ROS, the role of ROS in seed biology may need to be revisited. To date, many distinct roles for ROS, apart from their toxic effects, have been identified.

2. ROS and antioxidant system

Oxygen is an essential element for the life of aerobic organism but it may become toxic at higher concentrations. Oxygen molecule in its ground state is relatively unreactive; but its partial reduction gives rise to reactive oxygen species (ROS). ROS are highly reactive oxygen molecules consisting of free radicals. Free radicals are an atom or molecule having an unpaired electron which is extremely reactive, starting chain reactions that generate many more free radicals, that are capable of attacking the healthy cells, causing them to lose their structure and function [1–5]. Types of ROS include the hydroxyl radical, the superoxide anion radical, hydrogen peroxide, singlet oxygen, nitric oxide radical, hypochlorite radical, and various lipid peroxides [1–5] (**Table 1**). Reduction of oxygen leads to the formation of the superoxide radical ($O_2^{\bullet-}$), which is a molecule with an uncoupled electron and can react with other molecules to stabilize its energy. Hydrogen peroxide (H_2O_2) result from the nonenzymatic reduction of $O_2^{\bullet-}$ in the presence of H^+ ions, or from the action of catalase on $O_2^{\bullet-}$. H_2O_2 has a strong oxidizing capacity, and its life span is longer than that of superoxide. H_2O_2 can also diffuse through membranes and therefore reach target molecules at some distance from its production site [1–5].

Free radicals	Nonradicals
Superoxide, $O_2^{\bullet-}$	Hydrogen peroxide, H_2O_2
Hydroperoxyl, HO_2	Ozone, O_3
Peroxyl, ROO·	Singlet oxygen, $^1O_2$ or $^1\Delta g$
Hydroxyl, ·OH	Hypochlorous acid, HOCl
Alkoxyl, RO·	Peroxynitrite, $ONOO^-$

Table 1. Main reactive oxygen species (ROS) [1].

Enzymatic	Nonenzymatic or low molecular weight
Catalase	Glutathione (GSH)
Superoxide dismutase (SOD)	Ascorbic acid (vitamin C)
Ascorbate-glutathione cycle enzymes	Tocopherols (vitamin E)
Peroxidases	Polyphenols (flavonoids)
NADP-dehydrogenases	
Peroxiredoxin (Prx)	

Table 2. Main plant antioxidants [2].

The Haber-Weiss and Fenton reactions involve superoxide radicals and H_2O_2. In the presence of iron or other transition metals, $O_2^{\bullet-}$ and H_2O_2 lead to the formation of the hydroxyl radical, $OH^{\bullet}$, the most aggressive form of ROS, including the radical derivatives of oxygen ($O_2^{\bullet-}$, $OH^{\bullet}$), and also the peroxyl, alkoxyl or hydroperoxyl radicals, which are named as free radicals. Free radicals contain one or more unpaired electrons, but they also include nonradical derivatives of oxygen such as H_2O_2 and singlet oxygen [2, 5]. These free radicals are highly toxic and electrically charged molecules, i.e., they have an unpaired electron which causes them to seek out and capture electrons from other substances in order to neutralize themselves, all are capable of reacting with membrane lipids, nucleic acids, proteins and enzymes, and other small molecules, resulting in cellular damage, thus generate oxidative stress in plants [1–5].

Plants have developed a wide range of defense strategies to combat with these free radicals and deactivate their harmful effects known as antioxidants. The evolution of efficient antioxidant systems has enabled plant cells to overcome ROS toxicity and to use these reactive species as signal transducers [4, 5]. Antioxidants have diverse physiological roles in plants, acting as a scavenging and deactivating agent against oxidation, and converting the radicals to less reactive species, even at relatively small concentrations. The antioxidative system copes up with the harmful free radicals both by enzymatic (superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), glutathione reductase (GR), polyphenol oxidase (PPO), etc.), and by nonenzymatic (ascorbic acid (vitamin C); α-tocopherol, carotenes, flavonoids, polyphenolics, etc.) systems (**Table 2**). Under unfavorable conditions such as extreme oxidative stress, this antioxidant system scavenges the toxic radicals, and thus helps the plants to survive through such conditions [1–5].

3. ROS production in seeds

In plants, transport chain of electrons toward oxygen can potentially generate ROS. Seeds represent a particular case in this regard. During germination, the seed metabolic activity vary dramatically, meanwhile the sources of ROS in seeds also vary considerably [13, 39–45]. The mitochondrial respiratory chain is one of the major sources of ROS; electron leakage from the transport chain generates superoxide, and subsequently H_2O_2, by dismutation of the

former. During germination, respiratory activity increased and production of ROS enhanced [6, 14, 46, 47]. Another source of ROS is peroxisomes. Peroxisomes divided into: glyoxysomes (oily seeds), peroxisomes of photosynthetic tissues, nodule peroxisomes (*Fabaceae* nodules) and gerontosomes (senescing tissues) [14, 27, 46–50]. In glyoxysomes, lipid reserves of oily seeds are converted into sugars during the first stages of seedling development [49–51]. During this lipid oxidation process H_2O_2 is produced. In peroxisomal matrix, xanthine is also oxidized into uric acid by xanthine oxidase resulting with the production of superoxide [49–51]. Catalase (H_2O_2 eliminating enzyme) is localized in peroxisomes [49–52]. Production of nitric oxide (NO), (a free radical and also an important cellular signaling compound in plants) also takes place in peroxisomes [48, 51–54]. NADPH oxidases of the cell membrane are another sources of ROS in plants, these enzymes transfer electrons from cytoplasmic NADPH to oxygen, producing superoxide radical and its dismutating product H_2O_2. NADPH oxidases are increased during plant infections [28, 29], in plant growth processes [55], and under severe abiotic stress conditions [56]. Enhanced activity of NADPH oxidase is reported in ABA induced generation of ROS under water stress [57, 58]. During biotic stress cell wall peroxidases and amine oxidases are induced leading to the formation of H_2O_2 in the apoplast [59]. As a result, mitochondria and peroxisomes are the major sources of ROS in nonquiescent seeds, during seed development and germination. Aquaporins and peroxiporins (transmembrane proteins) are shown to play roles in the transport of H_2O_2 in vegetative tissues [56, 60], but the mobility of ROS in seeds has not yet been documented. Finally, lipid oxidation can generate ROS that could be trapped in seed tissues [16, 61].

4. The dual effect of ROS: from toxicity to signaling

4.1. Toxicity of ROS

The oxidative stress may cause damage to DNA resulting in cancer and aging [62], and the presence of reactive oxygen also may initiate a chain reaction at the cellular level resulting in damage to critical cell bio-molecules [63–65]. The uncontrolled accumulation of ROS, particularly of $OH^{\bullet}$ is highly toxic for the cell. These radicals are highly toxic and thus generate oxidative stress in plants. ROS can react with the majority of biomolecules, thus resulting in oxidative stress that can become irreversible and cause cellular damage [1–5]. Many harmful effects of ROS on cellular macromolecules have been identified [1–5]. All are capable of reacting with membrane lipids, nucleic acids, proteins and enzymes, and other small molecules, resulting in cellular damage [1–5]. Lipid peroxidation, which is a free-radical chain process leading to the deterioration of polyunsaturated fatty acids (PUFAs), is the best known cellular hazard among these, and has been studied intensively in food science [66]. Lipid peroxidation is initiated by free-radical attack upon a lipid, that gives starting to a chain reaction, removing a hydrogen atom from another fatty acid chain to form a lipid hydroperoxide (LOOH) in a propagation step [67]. This process is likely to degrade PUFAs present in membranes or in reserve lipids of oily seeds. Beside membranes, nucleic acids and proteins are also potential targets of ROS [67]. The hydroxyl radical, $OH^{\bullet}$, can damage both nuclear and organelle DNA directly, by having ability to attack deoxyribose, purines and pyrimidines [67, 68]. Enzymes

can also be inactivated easily by ROS, by degrading amino acids [69, 70]. ROS can damage transport proteins, receptors and ion channels and then lead to extensive cellular dysfunction [1–5, 69, 70].

5. The roles of ROS: cell signaling

Cellular antioxidant mechanisms control ROS concentrations, rather than to eliminate them completely, suggesting that some ROS may act as signaling molecules [5, 34–37, 46]. Although ROS have been considered as detrimental to seeds, advances in plant physiology evaluated them as messengers of various signal transduction pathways in plants. ROS are suggested as being beneficial for seed germination, seedling growth, protection against pathogens and controlling the cell redox status [28–40]. H_2O_2 is shown to be involved in the tolerance to various abiotic stresses acting as a secondary messenger [71], in cellular defense mechanisms against pathogens [72]. H_2O_2 has also been identified in many processes in plants, including programmed cell death (PCD) [8, 73], somatic embryogenesis [17], root gravitropism [19], and ABA-mediated stomatal closure [20, 21], response to wounding [74]. Superoxide ($O_2^{-\bullet}$) found to have roles in cell death and plant defense [24]. H_2O_2 also proved to have roles in protein phosphorylation through mitogen-activated protein kinase (MAP kinase) cascades [75, 76], calcium mobilization [77, 78], and regulation of gene expression [79, 80].

6. Control of ROS levels: detoxifying mechanisms

In plants and animals ROS are deactivated by antioxidants. These antioxidants act as an inhibitor of the process of oxidation, even at relatively small concentration and thus have diverse physiological roles [40]. Antioxidant constituents of plant materials act as radical scavengers, and convert the radicals to less reactive species [81, 82]. Plants have developed an array of defense strategies (antioxidant system) to cope up with oxidative stress. Plant cells are equipped with mechanisms allowing scavenging (in the case of oxidative stresses) or homeostasis of ROS (for cellular signaling) [83]. The antioxidative system includes both enzymatic and nonenzymatic systems. The nonenzymatic system includes ascorbic acid (vitamin C); α-tocopherol, carotenes, etc., and enzymic system include superoxide dismutase (SOD), Superoxide dismutase, which can be mitochondrial (MnSOD), cytosolic (Cu/ZnSOD) or chloroplastic (CuZnSOD, FeSOD), dismutates superoxide radicals into H_2O_2 and oxygen [84]. Hydrogen peroxide is eliminated by the action of catalase (CAT), which is located in glyoxysomes and peroxisomes [51]. The ascorbate-glutathione cycle (also called the Halliwell-Asada cycle) also takes part in H_2O_2 scavenging. Ascorbate peroxidase (APX), monodehydroascorbate reductase (MDAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) are involved in this cycle (**Figure 1**), and are present in chloroplasts, the cytoplasm, mitochondria, peroxisomes and the apoplast. These enzymes also participate in the regeneration of the powerful antioxidants such as reduced glutathione (GSH), ascorbic acid (vitamin C), and α-tocopherol (vitamin E) (**Figure 1**). Glutathione an

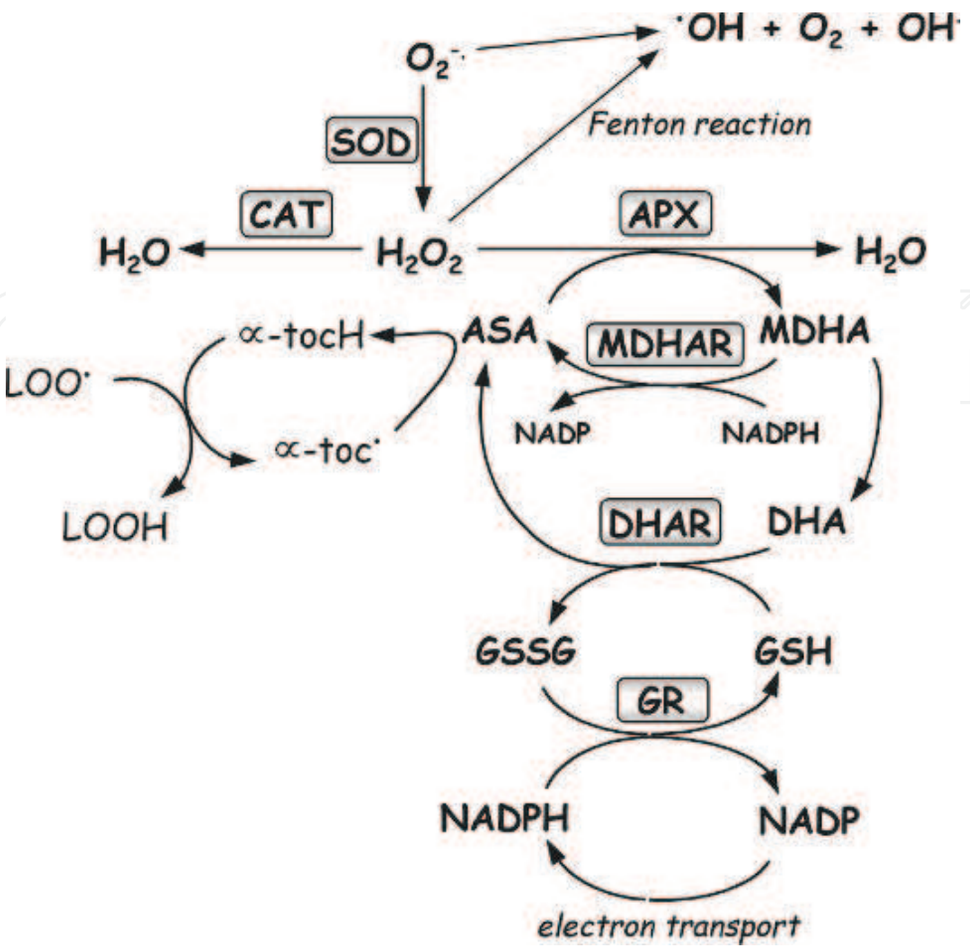

Figure 1. Main detoxifying mechanisms in plants. CAT, catalase; SOD, superoxide dismutase; APX, ascorbate peroxidase; MDHAR, monodehydroascorbate reductase; DHAR, dehydroascorbate reductase; GR, glutathione reductase; ASA, ascorbate; MDHA, monodehydroascorbate; DHA, dehydroascorbate; GSSG, oxidized glutathione; GSH, reduced glutathione; α-tocH, α-tocopherol; α-toc, α-tocopheryl; LOOH, lipid peroxide; LOO, lipid radical (Halliwell-Asada cycle).

important water-soluble antioxidant and is synthesized from the amino acids glycine, glutamate, and cysteine, which directly scavenges ROS such as lipid peroxides, and also plays a vital role in xenobiotic detoxification [85–88]. Research suggests that glutathione and vitamin C work interactively to quench free radicals and that they have a sparing effect upon each other [85–87]. Glutathione peroxidases (GPX) may also catalyze the reduction of H_2O_2 and hydroperoxides [85–88]. Polyphenol oxidase (PPO), the function of this antioxidant system is to scavenge the toxic radicals produced during oxidative stress and thus help the plants to survive through such conditions. Various compounds, such as polyphenols, flavonoids and peroxiredoxins [89] also have a strong antioxidant function.

7. ROS and seed development

Seed development consists of embryogenesis, reserve accumulation and maturation/drying on the mother plant, leading from a zygotic embryo to a mature, quiescent seed. During maturation

seeds undergo a period of desiccation where water content is reduced and the embryo is at a state of quiescence [10]. ROS are involved in final stage of seed development, in desiccation in tolerance. A dramatic loss of water becomes during desiccation or maturation phase which requires cellular adaptative mechanisms, at this stage ROS scavenging plays a key role, for allowing seed survival [10]. Recently, LEA (late embryogenesis abundant)-related proteins which are cited as accumulating proteins during drought conditions are correlated with desiccation tolerance, but their biological functions remain unclear [90]. A group-2 LEA class of proteins has been suggested to act as free-radical scavengers [91], emphasizing the importance of ROS scavenging in dehydration tolerance mechanisms. In developing or germinating seeds, the active mitochondria are probably one of the major sources of ROS, generating superoxide, and subsequently H_2O_2 [14, 32]. ROS is also generated in chloroplasts in the beginning of seed development, but they rapidly become nonfunctional [15, 63]. $O_2^{\bullet-}$ and H_2O_2 are produced in peroxisomes, and in seeds, glyoxysomes, which is a particular type of peroxisomes involving in mobilization of lipid reserves [15, 63]. High amounts of H_2O_2 are produced in glyoxysomes resulting from the activity of enzymes such as glycolate oxidase. H_2O_2 is known to promote seed germination of cereal plants, and exogenously applied H_2O_2 is shown to ameliorate seed germination in many plants [7, 92]. Ascorbic acid is the most important reducing substrate for removal of H_2O_2, acting as an antioxidant, in plant cells. It is reported that ascorbic acid suppresses the germination of wheat seeds, recently [93]. In plant cells, ascorbate peroxidase (APX) and catalase (CAT) that are involved in scavenging H_2O_2 are localized at the site of H_2O_2 generation [93] (**Figure 2**). H_2O_2 is mentioned to induce expression of many genes, coding defense-related proteins, transcription factors, phosphatases, kinases and enzymes involving in ROS synthesis or degradation [37, 54, 56, 79, 80] (**Figure 2**).

Seed filling is also associated with the high potential of the H_2O_2 detoxification machinery, mainly due to APX and CAT activities [94]. It is suggested that cellular membranes in germinating tissues are vulnerable to damage from desiccation [10, 69]. After the loss of desiccation tolerance several products of peroxidized lipids are accumulated [45], and activated forms of oxygen are generated through xanthine oxidase [35, 48, 50]. Some studies have also suggested

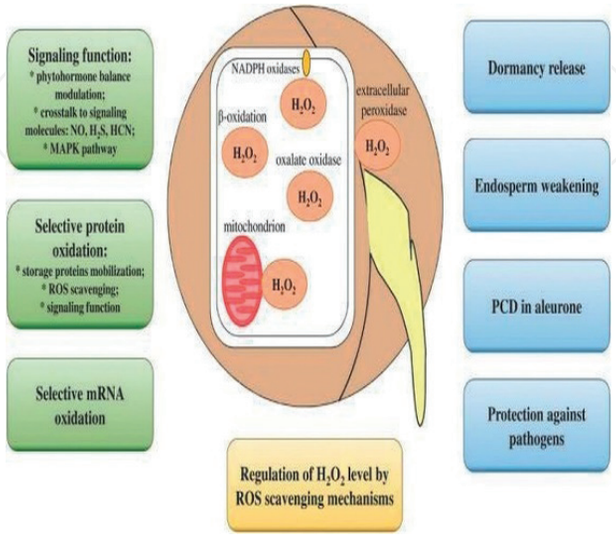

Figure 2. Production and functions of H_2O_2 in seed biology [37].

that ROS metabolism might also be important during initial embryogenesis [17, 95]. During embriogenesis, metabolic activity and mitochondrial respiration are increased, suggesting that developing embryos have the potential to generate significant amounts of ROS [17, 95]. The antioxidant ascorbate system reported to play an important role in embryogenesis and cell growth [41, 85]. Ascorbate content proposed to influence cell growth by modulating the expression of genes involved in hormonal signaling pathways [96]. Totipotency also related to antioxidant system, because of high ROS content and repressed expression of totipotency [97]. Conversely, ROS have beneficial effects in growth and development of plants. Seed germination requires release from dormancy. Treatment of dormant seeds with methylviologen (as a generator of ROS including $OH^{\bullet}$) is reported to break dormancy [98]. Hydroxyl radicals are also postulated to be involved in cell wall extension during cell growth, and auxin-induced increases in $OH^{\bullet}$ production is speculated to be involved in cell wall elongation, stiffening, and lignification depending on the concentration of auxin [55, 99]. Hydrogen peroxide is suggested to participate in lignin deposition in the cell walls in a peroxidase-catalyzed reaction [100]. The involvement of a diamine oxidase in H_2O_2 production has been demonstrated along with lignin deposition in the chalazal cells, in developing barley grains, in developing barley grains [100]. Production of ROS and their release in the surrounding medium are supposed to play a part in protecting the embryo against pathogens during seed imbibition [99]. Some of the selected published reviews on the dual roles of ROS in seed biology are listed in **Table 3**.

As shown above, the effects of ROS, and more particularly H_2O_2 on transcriptome have been widely studied [56]. However, up to date, there is no information available establishing a direct link between the changes in ROS content and gene expression during seed germination and development. Further experiments in this area, will be highly informative for getting a comprehensive view of ROS in seed biology.

ROS molecule	Physiological trait	Reference
Hydrogen peroxide (H_2O_2)	Alleviation of seed dormancy	Wang et al. [104]
H_2O_2	Somatic embryogenesis	Cui et al. [17]
Superoxide (O_2^-)	Plant defense response	Wisniewski et al. [24]
O_2^-	Survival and germination seeds	Roach et al. [105]
H_2O_2	Response to wounding	Oroczo-Cardenas et al. [74]
H_2O_2	Seed germination-ABA levels	Barba-Espin et al. [102]
Hydroxyl radical (OH^-)	Breakdown of polysaccharides	Schweikert et al. [106]
O_2^-	Cell growth by auxin	Schopfer et al. [55]
OH^-	Cell wall loosening	Müller et al. [107]
H_2O_2	Lateral root formation	Chen et al. [101]
H_2O_2	Seed germination via pentose phosphate pathway	Barba-Espin et al. [103]
H_2O_2	Programmed cell death	de Jong et al. [8]
O_2^-	Cell death	Doke et al. [22]

Table 3. Published reviews on the dual role of ROS in seed physiology [34].

8. Conclusion

ROS and antioxidants play important roles in seed biology. In seed life, ROS are involved in all the stages of seed development, from embryogenesis to germination. ROS can react with the majority of biomolecules, resulting in cellular damage. In developing or germinating seeds, major amounts of ROS are generated, which are highly toxic and thus generate oxidative stress in seed cells. Plants have developed an array of defense strategies (antioxidant system) to cope up with oxidative stress. Conversely, ROS are suggested to have beneficial effects in growth and development of seeds, and are considered as part of a signaling network involving in numerous regulatory components of seed development. For example, H_2O_2 is known to promote seed germination of cereal plants. The antioxidant system reported to play an important role in embryogenesis and cell growth. Ascorbate content is proposed to influence cell growth by modulating the expression of genes involved in hormonal signaling pathways. The above findings show that, these dual effects of ROS in seed biology are very interesting subjects and need further examinations for determination of the roles of ROS in seed physiology. Depending on the progress that has been required in seed tissue physiology, cellular production sites of ROS and their diffusion within the cell are established. Investigations in this field encourage to enlighten the cellular mechanisms involved in acquisition of the desiccation tolerance, germination and alleviation of dormancy. Finally, ROS signaling transduction pathway in seeds, from sensing to changes in gene expression, is not fully understood yet. Therefore, there is still a domain to be examined in future studies dealing with seed biology and ROS, which concerns the direct effects of these compounds on gene expression. Analyses of gene expression using the novel methods will be of help in elucidating the mechanisms underlying the interplay of ROS with hormones and their cross-talk in seed germination and development, providing a challenge for future research in this area.

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